

Burrows of desert-adapted frogs, *Neobatrachus aquilonius* and *Notaden nichollsi*

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Abstract

The non-cocooning frogs, *Notaden nichollsi* and *Uperoleia micromeles*, and the cocoon-forming frog, *Neobatrachus aquilonius*, burrow underground to survive in the hot, dehydrating arid interior of Australia. By four to six months after these frogs had burrowed, the only surface evidence that a frog had dug a vertical burrow was either a small raised-side crater ranging from 50 – 60 mm in diameter or a shallow depression the same size with a less compacted centre. *Notaden nichollsi* and *U. micromeles* were dug from poorly-defined, sand-filled burrows in sandy soil (1.4 – 4.1% clay and silt, 95.9 – 98.4% sand) at 600 to 2400 mm below the surface. Multiple *N. nichollsi* and *U. micromeles* were located in single burrows. In contrast, *N. aquilonius* were found in clay soil (12.5 – 17.9% clay and silt, 82.1 – 87.5% sand) in burrows 280 to 1200 mm deep. At a clay pan site only a single *N. aquilonius* was found in each well-defined, loosely filled burrow that we excavated. From a swale site, on one occasion we found two *N. aquilonius* in one burrow, and on another occasion we found a *N. aquilonius* and a *N. nichollsi* in the same burrow.

Keywords: frogs, arid, micro-habitat, Australia

Introduction

Arid-adapted frogs are abundant in many locations in the interior of Australia (Predavec & Dickman 1993; Morton *et al.* 1993). Despite this abundance we know little of the life history and ecology of these frogs. However, in recent years there has been a growing appreciation of the physiological and anatomical adaptations that enable some frog species to flourish in arid environments (Main & Bentley 1964; van Beurden 1977; 1982; 1980; 1984; Withers 1993; 1995; 1998; Withers & Thompson 2000; Bayomy *et al.* 2001). Most of what is known comes from laboratory experiments and indicates that there are two basic strategies to survive dehydrating arid environments. One group (including all *Cyclorana* spp. and *Neobatrachus* spp.) form a cocoon by continuously shedding multiple layers of skin (Withers 1995) and life underground is prolonged appreciably by a reduction of metabolic rate (Withers 1993) and tolerating dehydration (Main & Bentley 1964). An alternative strategy is to dig deep into the substrate but not to form a cocoon (including *Notaden* spp. and *Uperoleia* spp.). Much less is known about this latter group's anatomical, physiological and behavioural adaptations to their potentially dehydrating environment.

When frogs are surface-active following rain, it is often difficult to access their habitat due to local flooding and the impassable condition of unsealed roads. In addition, locating frog burrows during extended dry

periods is also difficult for the untrained observer and the task of excavating them can be arduous. There are only three brief reports on the burrows and microhabitats selected by arid-adapted Australian frogs (Slater & Main 1963; van Beurden 1984; Paltridge & Nano 2001).

During a field trip to the Kiwirrkurra Community in the Gibson Desert, Aboriginal women dug up a *N. nichollsi* from near the base of a sand ridge, many months after the last rain. We subsequently returned to Kiwirrkurra to draw on Aboriginal knowledge of arid-adapted frogs during June 2003 and again in September 2004. Our specific objective was to locate burrows and excavate frogs for the purpose of describing their microhabitat as they lay dormant underground.

Methods

During late June 2003, Aboriginals from the Kiwirrkurra Community (22° 49' S, 127° 47' E) took us to three locations for the specific purpose of locating *N. nichollsi* and *N. aquilonius*. We dug 22 frogs from burrows (a tunnel created by a frog that was loosely, passively filled with soil); six *N. aquilonius* and 16 *N. nichollsi*. We returned in September 2004, revisited these three sites and an additional two locations, and dug up another nine *N. aquilonius* and 12 *N. nichollsi*.

We recorded the surface habitat at the five sites (sites 1 and 2 were on sand ridges, site 3 was a clay pan, site 4 was a swale, and site 5 was the edge of dry creek bed) where burrowed frogs were excavated, and measured the depth of the frog below the surface. To quantify the difference in soil type between sites, soil samples were

taken from burrows adjacent to where we located three *N. aquilonius*, three *N. nichollsi* and a burrow in which we found a *N. aquilonius* and a *N. nichollsi*, and were used for soil particle size analysis (see Gilkes *et al.* 2000 for methods). Our analysis measured the proportion of sand, silt and clay in the substrate, which affects soil water retention properties and is particularly relevant to burrowed frogs. Soil temperature was measured at various depths by inserting a probe from a digital thermometer approximately 60 mm horizontally into the soil profile at various depths in the hole dug to retrieve the frog. Soil temperature profiles were taken for most burrows.

For *N. aquilonius* burrows, we either left the burrow intact, and dug around the hole (Plate 3), or dug down one side of the burrow, which enabled us to check for side burrows. Compaction of soil within the burrow was much less than for the adjacent soil, so it was easy to excavate the burrow and confirm the absence of side burrows. For *N. nichollsi*, we dug from one side of the loose, sand-filled burrow, leaving a semi-circular burrow evident on the unexcavated side (see Plate 7). The less compacted soil in the burrow made it relatively easy to excavate down a burrow.

We collected *N. nichollsi* that were surface active one night by searching with head torches.

Results

Residents at Kiwirrkurra indicated that the most recent heavy rain prior to our visit in June 2003 was in November 2002, and for our September 2004 visit, the most recent heavy rain had been during March 2004, so we estimated that about five months in 2003 and about six months in 2004 had elapsed since the frogs had burrowed.

Frogs were located at five different locations; two of these were sand ridges (sites 1 and 2), a clay pan (site 3), a swale (site 4), and the edge of a dry creek bed (site 5).

Neobatrachus aquilonius burrows

Fifteen *N. aquilonius* were excavated, with a mean snout-to-vent length of 40.0 (\pm 0.14) mm and a mean body mass of 10.2 (\pm 0.10) g. We found seven *N. aquilonius* in a clay pan (site 3; 22° 58' S 127° 54' E) that was sparsely vegetated with scattered mulga trees, tufts of grass and many large bare patches (Table 1; Plate 1). It had been burnt just before our 2004 visit and most of the ground litter and grass had been reduced to ash. Ash covered much of the ground which made it difficult to locate frog burrows. We excavated seven *N. aquilonius* in a swale (site 4; 22° 57' S 127° 53' E), which was about 200 m from a 7 m high red sand ridge. The swale was vegetated with groups of small trees, scattered shrubs, spinifex and the occasional Desert Oak. One *N. aquilonius* was excavated adjacent to Walla Walla Creek (site 5; 22°

54' 127° 40' E), which was a dry creek bed with steep sides (0.8 – 1.1 m).

Rain and wind damaged craters (Plate 2) or shallow depressions indicated where *N. aquilonius* had burrowed into the ground. Each crater or depression ranged in diameter from 50 – 60 mm. Burrows were vertical and the soil in each burrow was much less compacted than the surrounding soil. We either excavated each frog by digging adjacent to, or around the burrow, so as to not disturb or damage the frog when we eventually reached it (Plate 3).

The depth of the 15 *N. aquilonius* below the surface ranged from 280 to 1260 mm (Table 1). The maximum depth of the burrow was 750 mm in the clay pan, but *N. aquilonius* had deeper burrows in the less compacted soil of the swale (down to 1260 mm). There was no enlargement at the base of the burrows where *N. aquilonius* were located (Plate 3). Each burrow was filled with soil and each frog was in close contact with the loosely compacted soil at the bottom of their burrow. When a hole is dug adjacent to a burrow, the loosely compacted soil fell freely out of the hole, revealing its size and shape (Plate 3).

The clay pan (site 3) and the swale (site 4) had relatively high proportions of silt and clay (12.5 – 17.9% clay and silt, 82.1 – 87.5% sand) and were classified as 'clayey soils' (Table 2). Soil surrounding *N. aquilonius* burrows in the clay pan was much more compacted and difficult to dig in than in the swale. At Walla Walla Creek, the surface soil layer was a coarse sand over a deeper layer of coarser gravel. Surface soil temperature varied according to the time of the day it was measured. The clay pan (site 3) soil temperature ranged from 19 to 24 °C in June 2003 from 50 to 700 mm below the surface and it was about five °C higher in September 2004 (Fig. 1). Soil temperature in the swale (site 4) in September 2004 ranged from 25 – 27 °C from 20 to 120 mm below the surface (Fig. 1).

All *N. aquilonius* excavated at the clay pan (site 3) in 2003 and 2004 had a well developed cocoon that was thick enough for it to retain the shape of the frog after it was carefully removed (Plate 4). *Neobatrachus aquilonius* unearthed in the swale (site 4) and at Walla Walla Creek (site 5) in 2004 had very thin and flimsy layers of shed skin that were difficult to detect and which did not constitute a cocoon.

Notaden nichollsi and *Uperoleia micromeles* burrows

Twenty eight *N. nichollsi* were excavated at three locations (sites, 1, 2 and 4). Burrows containing *N. nichollsi* were located at the base, the face and on top of sand ridges. One *N. nichollsi* was found in a burrow with a *N. aquilonius*, in a swale about 200 m from the closest sand ridge (site 4). Site 1 (22° 48' S, 127° 48' E) was a red sand ridge adjacent to a swale that contained evidence of a temporary pond after heavy rain. The 5 – 10 m high

Plates. 1 – Clay pan in Mulga habitat typical of where *N. aquilonius* burrows were located; 2 – surface of a *N. aquilonius* burrow approximately five months after it burrowed; 3 – burrow of *N. aquilonius* in compacted clay showing the cocooned frog at the bottom (*n.b.* all the loose soil has run out of the burrow); 4 – cocoon from a *N. aquilonius* removed after approximately 6 months of aestivation; 5 – typical habitat for *N. nichollsi* and *U. micromeles* burrows; 6 – surface evidence of a *N. nichollsi* burrow, 7 – burrow of *N. nichollsi* that has been excavated to show its vertical orientation; 8 – *N. nichollsi* from the Gibson Desert.



Table 1

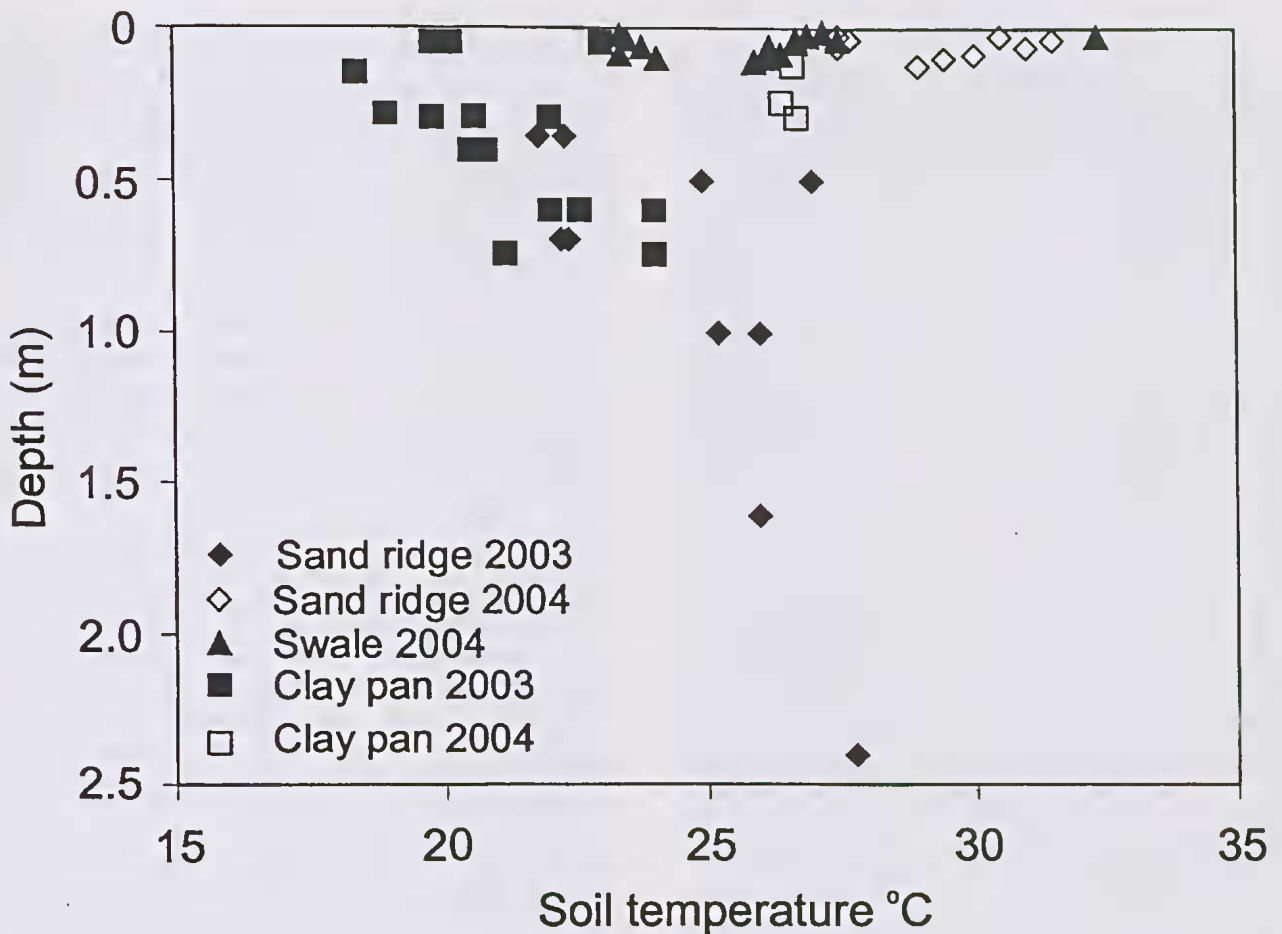
Number and depth of burrowed frogs, and surface habitat.

Month / year	Frogs found	No in burrow	Burrow depth (mm) at frog	Site ID	Location	Surface vegetation
Jul-03	<i>N. aequilonius</i>	1	600	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Jul-03	<i>N. aequilonius</i>	1	600	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Jul-03	<i>N. aequilonius</i>	1	600	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Jul-03	<i>N. aequilonius</i>	1	750	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Jul-03	<i>N. aequilonius</i>	1	750	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Jul-03	<i>N. aequilonius</i>	1	280	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Sep-04	<i>N. aequilonius</i>	1	300	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Sep-04	<i>N. aequilonius</i>	1	1200	Site 5	Walla Walla Ck	Under the edge of a large shrub, and tufts of grass
Sep-04	<i>N. aequilonius</i> / <i>N. nichollsi</i>	2	1120	Site 4	Swale	Scattered shrubs and spinifex
Sep-04	<i>N. aequilonius</i>	1	1260	Site 4	Swale	Scattered shrubs and spinifex
Sep-04	<i>N. aequilonius</i>	2	1100	Site 4	Swale	Scattered shrubs and spinifex
Sep-04	<i>N. aequilonius</i>	1	1200	Site 4	Swale	Scattered shrubs and spinifex
Sep-04	<i>N. aequilonius</i>	1	1100	Site 4	Swale	Scattered shrubs and spinifex
Sep-04	<i>N. aequilonius</i>	1	1000	Site 4	Swale	Scattered shrubs and spinifex
Jul-03	<i>N. nichollsi</i>	4	700	Site 1	Top of sand ridge	Scattered shrubs to 1.2 m, hole next to grass tufts, but exposed
Jul-03	<i>N. nichollsi</i>	1	700		Top of sand ridge	As above, burrows were about 100 mm apart
Jul-03	<i>N. nichollsi</i>	3	700	Site 2	Base of dune	Scattered shrubs to 1.2 m, scattered grasses and spinifex, hole under a low shrub
Jul-03	<i>N. nichollsi</i>	1	1600	Site 2	Two thirds the way up a sand ridge	Scattered shrubs and spinifex, hole found under over hanging <i>Acacia</i> branches
Jul-03	<i>N. nichollsi</i>	7	2400	Site 2	One third the way up a sand ridge	Scattered shrubs and spinifex, burrow in an exposed location
Jul-03	<i>U. micromeles</i>	2		Site 2		Same hole as above
Sep-04	<i>N. nichollsi</i>	1	730	Site 2	Two thirds the way up a sand ridge	Scattered shrubs and spinifex
Sep-04	<i>N. nichollsi</i>	1	1060	Site 2	Mid way up a sand ridge	Scattered shrubs and spinifex, burrow in an exposed position.
Sep-04	<i>N. nichollsi</i>	3	1450	Site 2	Top of sand ridge	Burrow in an exposed location
Sep-04	<i>U. micromeles</i>	3	750, 1000, 1450	Site 2	Top of sand ridge	Same hole as above
Sep-04	<i>N. nichollsi</i>	4	1530, 1530	Site 2	Top of sand ridge	Burrow in an exposed location
Sep-04	<i>U. micromeles</i>	2	1200, 1530	Site 2		Same hole as above
Sep-04	<i>N. nichollsi</i>	1	1000	Site 2	Top of sand ridge	Burrow in an exposed location
Sep-04	<i>N. nichollsi</i>	1	600	Site 2	Top of sand ridge	Burrow in an exposed location

Table 2

Composition of the soil from adjacent to *Neobatrachus aequilonius* and *Notaden nichollsi* when located in burrows. Mean ± 1 se in parenthesis; n = 3 for each cell.

Soil component	<i>N. aequilonius</i> burrows – clay soils			<i>N. nichollsi</i> burrows – sandy soils			<i>N. aequilonius</i> / <i>N. nichollsi</i> burrow
	Site 3	Site 3	Site 3	Site 1	Site 2	Site 2	Site 4
% clay and silt	13.0 (0.09)	17.9 (1.09)	12.5	1.6 (0.96)	3.4 (0.06)	4.1 (0.57)	14.2
% sand	87.0 (0.91)	82.1 (1.09)	87.5	98.4 (0.96)	96.6 (0.06)	95.9 (0.57)	85.8
Depth (mm) at which the frog was found and the soil samples were taken	1260	600	280	700	700	2400	1120



Discussion

In general, habitats selected by *N. nicholli* and *N. aquilonius* were very different. Our Aboriginal advisers indicated that *N. nicholli* and *U. micromeles* were always found near red sand ridges, adjacent to swales that had contained temporary ponds after heavy rain, whereas *N. aquilonius* were in clay soils that were sparsely vegetated with mulga trees and tufts of various grasses. We also found *N. aquilonius* in a swale about 200 m from a sand ridge. Soil particle size analysis indicated that the non-cocooning *N. nicholli* were found in sandy soils, whereas the cocoon-forming *N. aquilonius* were generally in clay soils (Table 2). Three *N. aquilonius* burrows at the clay pan (site 3) were within 1 m of a small mulga tree (site 3), but the others were more distant. Burrows of *N. aquilonius* on the swale did not seem to be located in any particular place (e.g. under a shrub, near trees, adjacent to spinifex).

Slater & Main (1963) reported finding *N. nicholli* and *U. mjobergi* in the same burrows, and Paltridge & Nano (2001) reported finding multiple *U. micromeles* and *N. nicholli* in the same sand-filled burrows. We also observed this genus association for three of our excavated burrows. Presuming that it is *N. nicholli* that actually digs the burrow, it appears that both *Uperoleia micromeles* and *U. mjobergi* are able to locate and dig into the burrows of *N. nicholli*. Whether this occurs at the time that *Notaden* dig the burrow, or sometime after it has been dug, is not apparent.

Non-cocooning frogs (*N. nicholli* and *U. micromeles*) presumably have a capacity to move underground should the soil conditions become unsuitable, but we found only vertical burrows and no evidence of lateral movement, even when there was more than one frog in the burrow. Side tunnels would have been easy to detect as the soil compaction in these burrows would have been less than in the surrounding soil. In one burrow, not all the *N. nicholli* were at the bottom, and *U. micromeles* were never found at the bottom of burrows. Slater & Main (1963) also reported that *U. mjobergi*, in the burrows with *N. nicholli*, were not located at the bottom. We presume that *N. nicholli* dug to a particular depth to gain access to moisture. If this is the case, then the reason why all frogs were not at the bottom of the burrow is not clear, as presumably the water management requirements of each species would be similar.

We were very surprised to find that *N. nicholli* had emerged and were foraging in the evening when there had been no overnight rain and only a small quantity of afternoon rain. This small quantity of rain presumably would not have penetrated more than a couple of mm into the soil and most would have evaporated soon after the rain clouds had passed. The environmental cue(s) for emergence of *N. nicholli* is not known. If *N. nicholli* emerge infrequently to forage on humid nights, then they could replenish their energy stores by feeding, and replenish their water stores while underground (Lee 1968). Cocooning species reduce their metabolic rate once the cocoon forms (Withers 1995), prolonging the period they can remain dormant underground. It is not known if there is a similar reduction in the metabolic rate by *N. nicholli* when they remain underground for an extended period, as occurs in *Scaphiopus* (Seymour 1973). If these

non-cocoon forming species do not reduce their metabolic rate, then they may be compelled to forage at the surface when conditions permit, and this may mean foraging on humid nights and when there has been little or no rain. If they do metabolically depress, then surface foraging during favourable conditions would further extend their survival period but would interrupt their metabolic depression and would incur an energy cost as frogs return to a depressed metabolic state over a number of weeks (Withers 1995).

It is likely that foraging under the conditions that we encountered *N. nicholli* would cause them to dehydrate rapidly and there would be a significant cost associated with again burrowing to a depth that would enable them to achieve water balance (unpublished data). The activity patterns and associated energetics of *N. nicholli* therefore appear to be a fertile area for future research.

As *N. aquilonius* form a cocoon at the bottom of their burrows they can not move underground to more favourable locations. Their inability to move once a cocoon has formed is probably not important as the cocoon significantly reduces water loss across the skin (the mouth and cloaca are sealed shut by the cocoon). We were very surprised to find a number of burrowed *N. aquilonius* at site 3 that had only a few layers of 'flimsy' shed skin indicating that cocoon formation had just commenced. If these frogs had burrowed soon after the heavy rains in March 2004, as was expected, and cocoon formation was at the rate reported by Withers (1995), then well-formed cocoons should have been evident. If the reason for the few layers of shed skin instead of a cocoon was that the soil water potential adjacent to the frog in the burrow was low enough for them to maintain water balance, then this would indicate that these frogs have the plasticity to switch between cocooning and non-cocooning strategies; such plasticity has not previously been appreciated, and this is an obvious area for further research.

The description provided by Slater & Main (1963) of the surface evidence that a frog has burrowed at a particular site (i.e. 'raised rim and loosely filled central crater') is similar to our observations for *N. nicholli* and *N. aquilonius*. Our Aboriginal guides were very skilled at detecting frog burrows, even after approximately five to six months since they had been made. After noting the specific surface characteristics of burrows that were pointed out to us by our Aboriginal guides, we were able to locate burrows of *N. aquilonius* and *N. nicholli* by ourselves.

The burrows of *N. nicholli* and *U. micromeles* were often deeper than those of *N. aquilonius*, and consistent with the depth of *N. nicholli* burrows reported by Slater & Main (1963) and Paltridge & Nano (2001). *Neobatrachus aquilonius* in the more compacted clay pan (site 3) had shallower burrows than those excavated in the swale (site 4). It is not known what influences the depth of the burrow dug by a frog. After heavy rain water would drain through the soil to lower levels and much would be lost by evaporation, so it would seem difficult for a frog to predict the water content (potential) for a particular depth months after a major rainfall event. Whether *N. aquilonius* dug deeper burrows in the swale because digging was easier than in the clay pan, or whether the depth was determined by some

environmental or physiological variable (e.g. energetic cost of burrowing) is unknown.

It is not known if *N. aquilonius* and *N. nichollsi* dig new burrows each time they become surface active or return to previously-used burrows. There is an obvious energy saving associated with burrowing into existing loosely-compacted burrows. However, relocating burrow openings at night might require frogs to have a 'mental' map of their activity area and the need to return to previously used burrows may limit the size of their activity area (i.e. there would be a high energy cost of returning to a burrow that is some distance away).

Water penetrates compacted clay soils slowly, compared with sandy or loosely compacted soils. It seems unlikely that rain would rapidly penetrate compacted clay soil to the depth of the frog, and stimulate it to escape from its cocoon, and dig its way to the surface so that it was surface active the first night after it rained. The shape of the burrow and the loose consistency of the soil in the burrow, compared to the greater compactness of the surrounding soil, provides an indication of how burrowed, cocoon-forming *N. aquilonius* are able to surface quickly after heavy rain. If a frog selects a burrowing site that is likely to have some run-on water, and pooling occurs on the surface even for a small time above the burrow opening, then water will percolate through the less compacted soil of the burrow down to the frog long before it penetrates down through the adjacent compacted soil to the same depth. In this way the frog's cocoon can become saturated, removed and eaten, and the frog surfaces and commences feeding, and perhaps even breeds, before water has soaked down through compacted soil to the depth at which it was burrowed. When a frog is ready to burrow again, it is likely that the surface water will have penetrated and softened the soil over a wider area and to a greater depth, making it much easier for the frog to burrow. Dimmitt & Ruibal (1980) reported that *Scaphiopus couchi* use low frequency sound or vibration as a cue for emerging from sandy soils. But it is difficult to imagine *N. aquilonius* removing and eating their cocoons, and digging their way to the surface in dry soil. Therefore, emergence stimuli for sand and clay burrowing frogs may be different because of the different rate that water percolates down through the soil profile.

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